

Prof. D. W. EWER
IN THE CHAIR.

Final
discussion

THE CHAIRMAN: In this final discussion we have an opportunity to compare and collate all the information presented at this meeting and to relate it to the broad scheme advanced by Professor Balinsky. In our previous discussions we have dealt with the causes and problems of animal distribution at different levels. We have considered actual distribution patterns, the factors behind these patterns and also the history and origin of the distribution. Sometimes these levels have been confused.

The matter is now open for discussion.

DR. WINTERBOTTOM: In connection with a north-east/south-west and north-west, south-east divide, Professor Balinsky has suggested that in the wetter periods the forest must have extended much further east than it does today. This is the assumption to which most workers have been driven by the facts of distribution. Recently, however, it has been much played down by others who suggest that if the forest was there at all in pluvial periods, it was only in small patches and wide dry areas must always have existed. Nevertheless one line of evidence strongly suggests that a broad band of forest did stretch from east to west. This is the degree of dichotomy which exists between the faunas of the savanna belt lying just south of the Sahara and of the savanna regions of southern and East Africa. This suggests that at some period the forest formed a barrier which savanna forms could not cross, splitting them into two groups, with isolation resulting in differentiation in some cases to the sub-specific and in others to the specific level. One example is our Cape Turtle Dove which is closely related to the Vinaceous Dove of West Africa. They were regarded first as con-specific but the weight of opinion now is that they are separate species. There are many other such cases in birds and probably other animal groups. This, in my opinion, is presumptive evidence that there was a forest barrier.

MR. STUART IRWIN: Chapin also suggests that the forest extended from the Belgian Congo through to East Africa. He argued that the distribution of the bustards and a number of other dry grassland forms pointed to separation. These forms are separated today not by forest but by moist savanna. This could well have been the case in earlier periods.

PROF. VAN ZINDEREN BAKKER: When we talk about forest I think we must draw certain distinctions, as there have been different types of forest. If we are to consider the heavy traffic

of animals up and down Africa, suggested by Professor Balmsky this morning, we must also postulate open routes. During the cold periods, that is, the more humid or hypothermal periods, there may not have been so many routes. On the central plateau a wetter type of savanna might have prevented movement north and south. On the escarpment and mountain areas there would have been a mountain forest; and, along the east coast, tropical rain forest of which at present there are relics. During a hypothermal period, therefore, there would not have been such possibilities for traffic by dry species. During the drier periods or non-pluvials, however, we have heard that there was a corridor going from the south-east to the north-west; and I myself have found some evidence of such a corridor at the southern tip of Lake Tanganyika. On the other hand, I would like to suggest the possibility of a coastal migration route. I wonder whether, during dry periods, we did not have much more open savanna country all along the east coast from, say, the Horn of Africa to Zululand.

MR. STUART IRWIN: My only reason for arguing against a dry coastal belt is the present existence of a rich and varied wood coastal avifauna, which could not have existed in dry savanna. Possibly, however, this fauna migrated across the plateau. We know that the fauna associated with Broken Hill man included oryx which are typical of the south-western Somali arid areas and also long-horned buffalo, which are probably open grassland animals.

DR. STUCKENBERG: Students of relict insects agree with the view that the forest extended across the African plateau. As far as the age of the African forest is concerned, various authorities are of the opinion that the forest in the Usumbara Mountains is of Miocene origin, basing this belief on the distribution of beetles.

DR. BIGALKE: The corridor theory is also supported by mammal and bird distribution. Benson and others produced a paper on birds in Salisbury last year in which they quoted a number of examples of pairs of closely related species or subspecies showing a gap in distribution from the north-east to the south-west. Amongst mammals the oryx shows this pattern clearly, with one species in the northern area and another in the southern region, ranging as far as Bechuanaland. There is also a record of Springbok remains in Olduvai Gorge, and the dameliskines show this type of distribution too.

DR. WINTERBOTTOM: I myself have no quarrel with a suggested route across this area which at the present moment consists of a band of savanna. However, the species pairs to which I originally referred, are not distributed north-east south-west and the barrier for them does not seem to be moist savanna. For instance, the Cape Turtle Dove goes right through the moist savanna and it and the Vinaceous Dove meet somewhere near Uganda. Thus no barrier exists at present.

DR. BRAIN: From a purely geological point of view there is very good evidence for a dry corridor in the distribution of Kalahari type sand, as mentioned in Dr. Cook's paper. These sands extend from the Kalahari north to the Congo, strongly suggesting a dry corridor in one of the interpluvial periods.

DR. STUCKENBERG: Could I ask Dr. Brain for his views on the date of the sands?

DR. BRAIN: The dating of such sand is very difficult because in effect the sand has always been there: it is immensely old. Thus it is really a matter of dating the redistribution, which probably happened on several occasions during the Pleistocene. The last major redistribution was immediately before the Gamblian period, say 50,000 to 100,000 years ago.

THE CHAIRMAN: We seem to have reached agreement on the existence of a dry corridor, but other questions remain. There is for instance, the problem of an archaic fauna which is so clearly shown in the arthropod groups; and we also have the question of a temperate fauna specific to the Cape. Is this temperate fauna an archaic one or has it come down from the tropical zone and re-adapted to the cooler area? I am thinking, for instance, of the widely distributed genus *Xenopus* which has temperate and also tropical species. Dr. Poynton suggests a temperate amphibian fauna but I do not know how this would relate to Gondwanaland. Perhaps Dr. Poynton would like to say something on this matter.

DR. POYNTON: There is one group which might throw some light on this, namely the genus *Heliophryne*. The group is most prominently found today in Australia and South America and there is an Eocene fossil from India, which must be post-Gondwana. This could possibly represent a Gondwanaland distribution or it might simply mean that the group was originally world-wide and has just been left in isolated regions. On the whole, I think that Darlington is right here, particularly in regard to the vertebrates, in leaving out the Gondwana story. As you know, he did not reject it entirely, but said it happened far too early to affect vertebrate distribution. In the case of the amphibia in the south-west Cape, there is no definite indication that any of the forms are from a Gondwanaland fauna. All could be derived from an earlier world-wide fauna, now restricted to certain areas, and now to be regarded as a temperate fauna, (a) because of its distribution pattern, and (b) its phylogeny. As with the north temperate fauna, there is a pronounced ancient element in the south-west Cape with a mixing of very old families and more modern groups.

PROF. BALINSKY: As the break-up of the continents occurred in the late Mesozoic, it is obvious that any remaining elements of a Gondwana fauna must have evolved before this time, in the first half of the Mesozoic. This is why the Gondwanaland fauna is mostly restricted to invertebrates, such as the more archaic arthropods, including the more ancient group of insects, and it would logically include the older fishes; but apart from *Protopterus*, the status of the Dipnoi is not very clear. Amongst the amphibia the frogs seem to have developed in the early part of the Mesozoic, so it is quite possible for them to have been a part of this Gondwana fauna, particularly *Heliophryne*.

I would like to point out an interesting ecological consideration. We know the tadpoles of *Heliophryne* are adapted to fast running mountain streams, and that is exactly the type of environment in which we find the palaeogenic insect larvae, the stone flies, and so on. This gives a fairly strong indication that this amphibian might be a relict of the Gondwana fauna. The fact that Leptodactylid frog remains have been found in India, is also a strong indication of this. As for reptiles, these are represented in South Africa by lizards and snakes which are more recent than the early Mesozoic. The mammals and birds could only be represented by more ancient forms amongst which the Ratitae may prove to be a Gondwana element. One suggestion of this is that, according to Professor Leymans the African ostrich and the South American ostrich have identical bird lice. Amongst the mammals of Africa, there seem to be two distinct strata, the ancient forms such as the Aardvark, the Scaly Anteater and the mongooses, and the more modern types, such as the large ungulates and the carnivores. There does not seem to be enough substance to prove that the edentate-mongoose fauna, if I might call it that, is a Gondwanaland element, although there are similarities to the South American fauna.

DR. POYNTON: Professor Balinsky's point about *Heliophryne* being found in running water is a very interesting one. However, many relict forms show a similar tendency, a preference for this type of environment. Furthermore, the fossil Leptodactylid which has been

mentioned is from the Eocene of India and could well point to a world-wide distribution of the family rather than a Gondwana distribution.

DR. OMER COOPER: No one has so far mentioned *Phreatoicus capensis*, a small crustacean living in pools in running streams. This animal has never had a world wide distribution as far as we know. Our species is variable but not divided into clearly defined forms and it extends all along the Cape sandstone zone on the sea side. A fossil species very closely allied in structure is found in Australia, and in New Zealand there are a dozen or so related genera and perhaps fifty species. Recently a species very near to *Phreatoicus* was found in India, and is being worked on and compared with our material at present. For various reasons this seems to be a good example of a Gondwana animal: it cannot fly; its eggs cannot be carried on the feet of birds because the female carries them; it also cannot be blown in the wind; and it dies in sea water.

DR. PLUMSTEAD: I think that one or two bits of geological and palaeo-botanical evidence on Gondwanaland may be of interest to zoologists. Recently I have been working on the fossil plants of Antarctica, and these are similar to those of the Cape from the lower Devonian and Bokkeveld. The coal plants from the late Carboniferous and the early Permian and Triassic plants are similar to those of our Molteno and lower Jurassic, and closely comparable to those of the older parts of Gondwanaland. It would appear that Africa broke away at the end of the Jurassic. Further Africa seems to have broken away first, and to have moved northward. A cold temperate flora developed in the rest of Gondwanaland including *Motophagus* and *Auracius* which were common to South America, the Falkland Islands, Australia, and even India. So there should be a faunal tie-up of animals that were common to Africa up to the late Jurassic, and not common after that time.

DR. STUCKENBERG: Dr. Plumstead's account seems to tie up in many different ways with the distribution of invertebrates, in particular with those paleogenic groups which live in cold mountain streams. There are very few of these in South Africa compared to the tips of other continents. Australia, New Zealand and South America have many more and they have many more in common with one another than they do with South Africa. This would make sense, following Dr. Plumstead's remarks.

A curious thing about these elements in South Africa, is that their affinities lie almost invariably with Australia, Tasmania and New Zealand and not with South America. This is a well marked feature and it is really quite an event to find a paleogenic animal related to South America.

PROF. WELLS: I would like to return to a point made by Professor Balinsky about the older and younger strata in the mammalian fauna of South Africa. We may perhaps call these the pre-Miocene and the post-Miocene strata, the first consisting of generally archaic forms derived from rather unspecialized groups (although they have produced some very specialized representatives, as among the insectivores, for instance), and the second, post-Miocene strata consisting especially of the dominant ungulates. But I would like to suggest further that there were probably several levels within these major divisions, especially in the post-Miocene group. Among the antelopes, we can possibly recognize earlier and later elements, in the sense that there are certain antelope groups which have always been confined to Africa (the Duikers and the Neotragines, for instance), whereas the other antelope groups have included Eur-African and Eur-Asiatic members. During the later Miocene and Pleistocene they gradually became narrowed down to Africa. From that, I would like to go on to tie up with what I think was Dr. Winterbottom's original point about distribution in Africa,

because one particular group, the Hartebeest, illustrates his point very well. We have a belt of related species of Hartebeest (some people say only sub-species), crossing the savanna belt south of the Sahara with some differentiation from west to east and we have what appears to be a reasonably closely related form, the Red Hartebeest in Southern Africa. Interposed between the two, we have the quite distinctly divergent Lichtenstein's Hartebeest.

We do not know enough about the paleontology of these animals to work up a theory as to how this differentiation has come about, but we are aware that during the early Pleistocene, there was an extraordinary accumulation of Hartebeest-like fossil antelopes in southern and East Africa. In fact, there were probably twice as many genera and species as we have in the later Pleistocene and Recent. Possibly as we get to know these forms better, some theory will emerge.

DR. WINTERBOTTOM: I should like to make one small comment about the Ostrich and the South American Rhea. In the Tertiary, the Ostrich was not confined to Africa, but was found in central Asia as well. If it was a Gondwanaland relic, it must have got out of Gondwanaland and have spread into what is now the whole Arctic region. This does not necessarily invalidate the suggestion that the Ostrich and Rhea may be Gondwanaland relics, but it is perhaps a modifying factor.

PROF. BALINSKY: I don't think this is a contradiction because the Ostrich has obviously emancipated itself from the complex of temperate forms and gone over into the tropics, at least the dry tropics. Then, of course, its limit of distribution was the end of the northern continent with which at that time Africa must have had a connection.

THE CHAIRMAN: We seem to go constantly back to Gondwanaland and I want to put my problem once again. I don't really feel that Dr. Poynton clearly answered the question. He spoke of the possibly Gondwana origin of some amphibia, but I would like to know whence come the non-Gondwana-elements in the south temperate fauna of the Cape today. Do they have a tropical origin or was there at some earlier period a connection with the north-temperate fauna? The fact that the northern-temperate regions and the southern temperate regions show similar constitution, seems to me to provide a problem which lies somewhere between Gondwanaland and the more recent period. Are you willing to answer this, Dr. Poynton?

DR. POYNTON: Here I follow Darlington, believing that the world fauna as a whole emerged in radial waves of distribution from tropical regions, more particularly those of Africa and India; and with these waves there were movements to more unfavourable areas, both north and south. I think the Amphibia provide very convincing evidence for postulating such waves, and also for supposing that before one wave has reached the final backwater—let us say in South America—the next wave is on the way already. I would therefore say that the fauna of the South-west Cape has been derived from the northern equatorial areas and this fairly recently. By now these forms have been ousted from equatorial regions by new forms, but they are still preserved in extra-tropical areas. The distribution of *Heliophryne* can be explained in this way, and I think the theory probably holds good for the vertebrates as a whole.

DR. WINTERBOTTOM: There is one point about Darlington's theory which might be elaborated a little because it is an aspect which is not always clearly understood. Many workers believe that this theory postulates a general pattern of distribution and succession whereby the primitive forms get pushed out to unfavourable environments and left there, while the highly evolving centres contain the newest forms. However, Darlington himself in, I think,

his most recent paper has pointed out that this is by no means the invariable rule. On the contrary, very many primitive forms remain in the tropical areas after they have died out in more temperate regions and Darlington explains the extraordinary richness of the tropics by saying that they include:

- (a) newly evolved forms which have not had time to spread outwards as yet;
- (b) forms that have already spread over the temperate and the tropical areas;
- and (c) more primitive forms which have been extinguished in the temperate zones but have managed to find a niche to hang on to in the tropics.

MR. STUART IRWIN: I would like to point to a group that is abundant in your Cape region but that does not appear to be a relict. I refer to the genus *Serinus*, an abundant one, not only in species but also in individuals. Further north in the tropics, the serins are replaced by weavers and waxbills. Both groups are basically rather similar in habits, both are equally advanced, and yet one excels in a temperate climate and one in a tropical. Here then we have in the serins a group which could be taken as a relict (but I personally do not think it is), and they have relatives in the Palearctic, and the Nearctic and many species throughout the rest of Africa, especially on the mountains.

DR. WINTERBOTTOM: The Fringillidae are essentially a temperate group because there are, in addition to a few widespread species in tropical Africa, others which occur in the tropics but only in the temperate parts of it, that is to say, on the mountain tops. They are the most numerous, I think, of all the Passerine bird families. They have more species in the whole Arctic region than any other Passerine family and they are also extremely abundant in North America.

PROF. WELLS: I would like to put a question which I hope Dr. Plumstead will be able to answer for me regarding the geological history of Africa.

I seem to recollect, having heard it said on an earlier occasion by Dr. Cook, that there has been a great deal of up-warping of the African continent in the latter Tertiary, since the Miocene, and that there has been an elevation of some thousands of feet in inland plateau areas. It seems to me that, if that is the case, it must have effected quite considerable changes in the climate of the continent and it may well have upset our distribution area quite considerably as compared with the early Tertiary. It may also have had the negative effect, which bothers us so much, of preventing any deposition of Pliocene deposits.

DR. PLUMSTEAD: Professor Wells' point about up-warping is of very great importance in the preservation of fossil life right through Africa's history. Professor Holmes of Edinburgh has recently published a map in which he shows that Africa has always had what he calls "a basin and a swell" structure: a series of basins separated from one another by high connecting ridges. This characterizes the structure from pre-Cambrian times. For the fossil record, this is extremely important because, even in periods of uplift, Africa has never been a crumpled area. The whole region has in fact, been subjected to movements upward and downward, and not to orogenic movement, except in the Atlas mountains and the Cape fold belt. The basins have preserved some remnants for us even on the highest portions. Apart from them the continent would have been scoured down to its granite basement throughout instead of just in patches.

DR. STUCKENBERG: Perhaps I may venture some comments too. A very significant feature in the geological history of Africa is the complete reduction to a peneplain by the end of the mid-Miocene. Various estimations have been made as to the elevation of this peneplain.

These are generally rather low but I have seen one calculation which gives the maximum elevation at 2,000 ft.

To go back to Professor Wells' question: this peneplain has been elevated at least three times, the first elevation occurring in the mid-Miocene, the second in the Pleiocene and the third in the Pleistocene. There seems no agreement between various authors as to the extent of the elevation on each occasion. Probably the greatest extent of African forestation was achieved at the close of that planation in the mid-Miocene. It seems possible to me that this offers a not unreasonable explanation of the distribution of mammals or at least the ungulate mammals.

MR. GRINDLEY: I would like to return briefly to the point made by Professor Omer-Cooper, regarding the crustacean *Phreatoicus*. I think we have to be very careful here about suggesting that these little crustaceans were limited to the Gondwana area. There is for instance another similar genus, *Protojanira*, which now has three species found in South Africa in the mountains of the south-west Cape and in the Drakensberg; and there are forms fairly close to this which are found widespread in the deepest oceans. It seems clear that these forms are relicts of a primitive group and it seems that the distribution of these groups was once far more widespread than merely the Gondwanaland continent. The absence of fossils of forms as small as this is not a good indication that they were not more widespread in earlier times.

THE CHAIRMAN: Professor Balinsky mentioned the importance of barriers in the development of species and the limiting of gene flow; and one of the questions which seemed to me to have been little discussed is the dynamics of speciation. I wonder if there is anyone who has any feelings to express about this and also of the importance or otherwise of trying to recognize generalized climatic or biotic factors determining distribution.

DR. POYNTON: As regards speciation, there is a point which might be brought to the attention of workers in Africa studying distribution. This is the work of Brown in America, on what he calls centrifugal speciation. I do not know whether the members of this gathering are familiar with his paper which appeared some two years back. It seems that we have in this country enormous scope for studying the problem of centrifugal speciation in that we have an apparently robust centre of speciation in Central Africa. The limits of this centre are clearly marked by some quite marked changes in climate which cause an expansion and contraction in the tropical fauna and flora, producing conditions most favourable for the development of species at the periphery, as opposed to the more generalized changes which take place—or are supposed to take place—in the central area. I have no information myself which might contribute to Brown's idea but I think the attention of workers could be drawn to this very interesting theory.